Grazing preferences of *Onychiurus armatus* (Insecta: Collembola) for mycorrhizal and saprophytic fungi of pine plantations

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INTRODUCTION

It is well established that mycorrhizal infection of plant roots is beneficial to the host plant (Harley 1969), generally due to an increased supply of phosphate (Mosse 1973). The fungal hyphae increase the volume of the depletion zone around the roots, thus increasing the labile phosphorus pool available to the plant (Tinker 1975). Clearly, it is of interest to investigate the factors affecting the size of the depletion zone, and one such factor could be arthropod grazing of the hyphae.

It has been shown that the presence of Collembola in a microcosm experiment reduced the benefits of endomycorrhizal infection to leeks (Warnock, Fitter & Usher 1982), apparently by grazing of the hyphae. Although endomycorrhizal fungi are the most important mycorrhizal symbionts of most plant taxa, the principal mycorrhizal associations of trees are the sheathing or ectomycorrhizas. No work has yet been published on the effects of arthropod grazing on ectomycorrhizal fungi, despite observations that aphids (Zak 1965) and protura (Nosek 1977) suck on ectomycorrhizal sheaths. This paper presents two preliminary lines of investigation relevant to this problem: (i) surveying of the Collembola and fungal communities in a series of pine stands, and (ii) choice experiments using field-collected Collembola and a range of isolates of fungi characteristic of pine forests. The aim of the field survey was to identify the dominant species of Collembola and fungi in the pine plantations, and that of the choice experiments was to determine whether a consistent hierarchy can be found in feeding preferences between fungi.

SITE DESCRIPTION AND METHODS

Fieldwork, based at Spadeadam Forest, Northumberland (National Grid reference NY620740), lasted from 13 September to 16 November 1983. The forest is at an altitude of approximately 300 m, and is mainly lodgepole pine (*Pinus contorta* Dougl.) and Sitka spruce (*Picea sitchensis* (Bong.)). The soil is an acid peat, pH 3·8 ± 0·3, with acetic acid extractable phosphorus (after Allen 1974) 12·6 ± 16·9 mg 100 g^{-1} (mean ±SD, pooled results for seventy-five soil cores). Analyses were performed with the facilities and help of the Chemistry Section at ITE Merlewood.

All fieldwork was done in ten stands of *P. contorta*, representing two replicates

of five ages (12, 15, 19, 23 and 26 years). In each stand, sampling was confined to a staked area 10 m square, at least 2 m in from the stand edge (except for one stand where this was not possible). The site was visited weekly, when three stands were sampled, so that each of the ten stands was visited three times during the sampling programme. During sampling, six soil cores (6 cm diameter × 9 cm deep) were taken midway between randomly chosen trees. A 50 cm quadrat was centred on the core location, and two sets of observations were made: the number of sporophores of each saprotrophic fungus in the quadrat, and the number of sporophores of each mycorrhizal fungus within 3 m along the planting ridge. Soil cores were returned to ITE Merlewood upright and intact, then divided into three layers, each 3 cm thick, prior to extraction of the Collembola in a portable high gradient extractor (Usher & Booth 1984).

The choice experiments were carried out using *Onychiurus armatus* (Tullberg) *s. lat.*, being the only dominant Collembola amenable to laboratory culture. The fungi came from stock cultures from ITE Merlewood except for *Marasmius androsaceus*, *Mycena galopus* and *Lactarius rufus* which were isolated from material from the field site during autumn 1983.

All experiments were carried out in 5 cm diameter pill boxes floored with 3 mm of 10:1 plaster-of-Paris:charcoal (Goto 1961). Three holes of 8 mm diameter were sunk in the floor, into which were fitted 8 mm cores of agar so as to be flush with the surface. Two of the agar cores were from cultures of the fungi to be tested, while the third was a sterile control. Twenty Collembola were introduced into each chamber, and the number apparently feeding on each fungus was recorded three times per day. The experiments were kept at 15°C and lasted up to 5 days. At the end of each experiment the number of Collembola alive and dead, the number of faecal pellets present on each agar disc, and the estimated area of each disc remaining ungrazed were counted or estimated.

RESULTS

The site held two dominant and three less common species of mycorrhizal fungi, of which *Lactarius rufus* was the commonest and most widely distributed, although it was recorded most frequently in the younger stands (see Table 1). *L. rufus* is also the only mycorrhizal fungus which has been isolated from Spadeadam material. This is not unexpected since mycorrhizal fungi are typically difficult to isolate (Chu-Chou & Grace 1982; J. Dighton, pers. comm.).

Four species of saprotrophic fungi were recorded, of which two were recorded only once. The commonest species was *Marasmius androsaceus*, while *Mycena galopus* was recorded occasionally. Preliminary results of the Collembola survey indicate that *Onychiurus armatus* (Tullberg) *s. lat.*, *Friesea mirabilis* (Tullberg), *Folsomia brevicauda* Agrell, and *Pseudisotoma sensibilis* (Tullberg) are the most frequent species.

TABLE 1. A list of the species of fungi recorded from a survey of *Pinus contorta* stands in Spadeadam Forest during Autumn 1983. The list contains the number of quadrats where each species was recorded (total number of quadrats is 180), the total number of sporophores counted, and the percentage found in each stand age

	Number of records	Number of sporophores	% of sporophores found in stand age (years)				
			12	15	19	23	26
Mycorrhizal species							
Lactarius rufus (Scop. ex Fr.)	56	222	67	15	10	8	< 1
Inocybe longicystis Fr.	33	88	8	36	2	43	10
Russula emetica (Sceaff. ex Fr.)	9	27	0	69	0	26	15
Laccaria laccata (Scop. ex Fr.)	6	15	7	87	7	0	0
Saprotrophic species							
Marasmius androsaceus (L. ex Fr.)	72	420	22	29	41	2	6
Mycena galopus (Pers. ex Fr.)	12	23	22	7	11	11	48

To date the choice experiments have been run using twelve species of fungi. Table 2 lists the preferences between the eight fungi most intensively studied. From the present results, *L. rufus* would appear to be the most highly preferred species.

DISCUSSION

The fungal community of the field site is depauperate compared to that found in a deciduous wood, but is typical of upland pine plantations on acidic, nutrient poor soils (J. Dighton, pers. comm.). Although the Collembola species composition is

TABLE 2. The relative preferences* shown by *Onychiurus armatus* for eight cultured fungi: three of these (*M. androsaceus, M. galopus* and *M. epipterygia*) are saprotrophic, the others are mycorrhizal

	Fungal species (first letters of generic and specific names)							
	Lr	Ma	Sl	Mg	Me	Pi	Rl	Hc
Lactarius rufus (Scop. ex Fr.)	0	+	+	+	+	+	+	+
Marasmius androsaceus (L. ex Fr.)	<	0	=	+	+	+	+	+
Suillus luteus (Fr.)	<	=	0	+	+	=	+	+
Mycena galopus (Pers. ex Fr.)	<	<	<	0	=	+	+	+
Mycena epipterygia (Scop. ex Fr.)	<	<	<	=	0	=	=	+
Paxillus involutus (Fr.) Fr.	<	<	<	<	=	0	+	=
Rhizopogon luteolus Fr.	<	<	=	<	=	<	0	=
Hebeloma crustuliniforme (Bull. ex St. Amans)	<	<	<	<	<	=	=	0

* In the table the vertical axis will be referred to as the *Y* axis, and the horizontal axis as the *X* axis. The following symbols are used:

0 not a comparison;
= no significant preference between fungi;
\+ *Y* axis fungus is preferred to *X* axis fungus;
< *Y* axis fungus is avoided relative to *X* axis fungus.

only known approximately, it is comparable with other studies of upland Collembola communities (Usher 1967; Hale 1966).

It is well established that Collembola may exhibit significant preference betwen fungi (McMillan 1976; Visser & Whittaker 1977; Newell 1980), but no work published previously has shown that these preferences may be organized into a consistent hierarchy. The two most highly preferred fungi (*L. rufus* and *M. androsaceus*) are the two likely to have the highest hyphal densities in the field, assuming that hyphal density may be inferred from sporophore frequency.

The results presented here agree with Newell (1980), using *Onychiurus latus* Gisin, who found that *M. androsaceus* was significantly preferred to *M. galopus*, both in laboratory choice experiments and in the field. She also found that selective grazing by *O. latus* altered the outcome of competition between these fungi both in the laboratory and in the field. Parkinson, Visser & Whittaker (1979) also showed that selective grazing by Collembola of the genus *Onychiurus* could affect the outcome of competition between saprotrophic litter fungi. This suggests that a similar effect may be noted with mycorrhizal fungi. Certainly *L. rufus*, a mycorrhizal species highly preferred by *O. armatus*, was the dominant symbiont in stands up to 12 years old and declined in importance thereafter (Table 1). Succession is a well documented phenomenon in ectomycorrhizas (Marks & Foster 1967; Dighton & Mason, in press) but no work published so far has suggested the possibility that arthropod grazing may be involved.

The pronounced preference shown by *O. armatus* and *L. rufus* hyphae combined with the wide distribution of both species in the field suggests that mycorrhizal grazing is most likely to occur to some extent. Any such grazing will reduce the mean length of the mycorrhizal hyphae, thus the volume of soil available to the root system. The results of Warnock *et al.* (1982) indicate that even a moderate level of hyphal grazing might have a deleterious effect on the plant, although the two systems are so different that accurate analogies may not be drawn.

As a final observation, the three least preferred fungi are known to contain toxic compounds: *H. crustiliniforme* and *P. involutus* are known to be dangerously poisonous to man due to high concentrations of muscarine and other toxins, while *R. luteolus* is little known but reported to be toxic to slugs (S. Visser, pers. comm.). This may indicate that these fungal toxins protect the hyphae in the soil against grazing arthropods, and that the toxicity of the sporophore hyphae is secondary or even incidental. The results of Lacy (1984) show that sporophores are not protected from mycophagous *Drosophila* by secondary toxins, while the results presented above suggest that toxins may protect mycelial hyphae from grazing by *Onychiurus*.

This hypothesis predicts that fungi whose hyphae ramify through decaying wood, where few if any arthropods can penetrate, should not possess secondary toxins since the hyphae have no need of protection. A limited search, using Phillips (1981) indicated that no British wood-decaying fungi are poisonous, although many are classed as 'inedible' due to the hardness of the sporophore.

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